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Long-term succession of aquatic plants reconstructed from palynological records in a shallow freshwater lake

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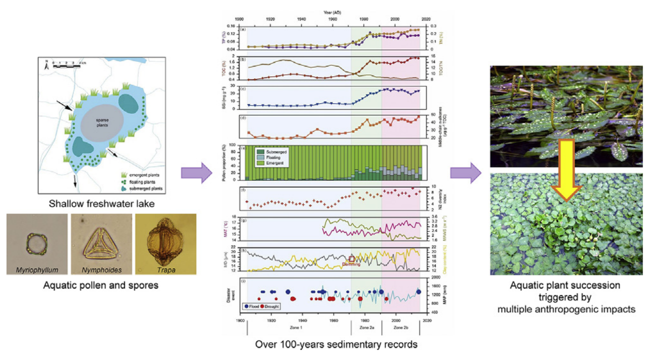
HIGHLIGHTS

- First attempt to reveal long-term aquatic plant succession in the MLYB based on palynology.
- There was a low biomass of aquatic plants in Changdang Lake in the first half 20th century.
- Changdang Lake is currently in a macrophyte-algae transition.
- Hydrological condition and nutrient input are the main factors for succession of aquatic plants.
- The 1970–1980s state of aquatic plants in Changdang Lake would be a realistic restoration target.

GRAPHICAL ABSTRACT



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ABSTRACT

Aquatic plants in shallow freshwater lakes play a key role in stabilizing ecological function and providing valuable ecosystem services, yet they are severely degraded worldwide. An improved understanding of long-term aquatic plant succession is critical to investigate the potential driving mechanisms and to facilitate ecological restoration. In this paper, we reconstructed changes in the aquatic plant community over the past century based on palynological records from Changdang Lake, Middle and Lower Yangtze River Basin (MLYB), China. Our results reveal that aquatic plants in Changdang Lake have undergone three clear phases: emergent macrophytes dominated the aquatic vegetation in the 1900s–1970s, submerged macrophytes in the 1970s–1990s, and floating macrophytes increasingly after the 1990s. Significant changes in the aquatic plant communities were caused by increasing anthropogenic pressures, such as damming and nutrient loading from agriculture, aquaculture, and urbanization after the Chinese economic reform. We argue that Changdang Lake is currently in a transition phase between a macrophyte-dominated state and an algae-dominated state. Our palynological record is different from many contemporary studies, which suggest submerged plants dominated most lakes in this region before the 1950s. We suggest that the return of the aquatic plants to their 1970s–1980s state would be a realistic target for lake restoration. Our results show that palynological records can reveal long-term dynamics of macrophytes in shallow lakes for sustainable lake restoration and management.

1. Introduction

Shallow freshwater lakes have been supported human livelihoods for millennia, yet today most of these freshwater ecosystems are

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suffering severe degradation worldwide due to increasing anthropogenic pressures (Millennium Ecosystem Assessment, 2005; Wang et al., 2014; Hou et al., 2017). Aquatic plants play a key role in stabilizing lake ecosystems and providing valuable ecosystem services, e.g. increasing water quality and clarity, stabilizing bottom sediments, decreasing the rate of nutrient cycling and providing food and habitats for aquatic animals (Dennison et al., 1993; Jeppesen et al., 1998; Li, 2014; Zhang et al., 2017). Numerous studies show that widespread degradation of aquatic plants in many shallow lakes has accelerated during the past century with severe consequences for lake functionality and stability (Sand-Jensen et al., 2000; Arts, 2002; Moss et al., 2011; Phillips et al., 2016; Hill et al., 2017). According to a recent investigation, decreasing aquatic plants are found in around 65.2% of the world lakes, and the loss of submerged plants accounts for >65.3% of all aquatic plants (Zhang et al., 2017).

Eutrophication is a major reason for the loss of submerged plants, particularly in shallow lakes (Best et al., 1984; Körner, 2002; Qin et al., 2013). Increasing nutrient input may trigger a shift from a clear macrophyte-dominated state to a turbid algae-dominated state (Scheffer et al., 2001; Carpenter, 2003; Scheffer and Jeppesen, 2007; Phillips et al., 2016). Such a catastrophic shift causes extensive biodiversity loss and eventually the collapse of the whole aquatic ecosystem, and it is extremely difficult to restore ecosystems that have been severely disturbed (Wang et al., 2015). Understanding the long-term change of aquatic plants can generate crucial information for lake restoration and management (Mcgowan et al., 2005; Ayres et al., 2008). Yet, little is known about the nature, direction and sequence of such change over multi-decadal timescales, especially the ecological mechanisms for the decline in aquatic plants in different stages (Sayer et al., 2010; Phillips et al., 2016).

The current understanding of the long-term variability of aquatic plant communities are mainly based on historical records (Sand-Jensen et al., 2000), field surveys (Egertson et al., 2004; Dong et al., 2014), and remote sensing images (Gullström et al., 2006; Liira et al., 2010; Villa et al., 2015). For example, Luo et al. (2016) successfully used remote sensing records to reconstruct aquatic vegetation change in Taihu Lake from 1984 to 2013, finding that submerged plants increased before 2000 and then decreased during the last 10 years. Nevertheless, the above-mentioned methods have limitations. Historical records and field surveys are unable to record continuous aquatic plant variability through time. Remote sensing images only capture the aquatic plant information within the last three or four decades (Luo et al., 2016). These methods are all unable to reconstruct comprehensive and continuous records of aquatic vegetation change over longer timescales. Instead, pollen and spores of aquatic plants can be identified at genus level and preserve well in lake sediments (Zhao et al., 2009; Ge et al., 2017), ensuring the robust species richness and time continuity for reconstruction. Thus, palynological records can effectively reconstruct valuable information about the changing biological structure and function of macrophytes (Sayer et al., 2010). However, there have been few attempted studies focusing on pollen-based aquatic plant reconstructions around the world (Davidson et al., 2005; Yang et al., 2017).

The Middle and Lower Yangtze River Basin (MLYB) in China holds approximately 5900 freshwater lakes, ponds and reservoirs, covering 15,000 km^2 and accounting for about 25% of the freshwater resources in East Asia (Wang et al., 2014). However, in the last four decades, lakes in the MLYB have gone through different eutrophic stages with various degrees of aquatic vegetation loss (Qin et al., 2013; Zhang et al., 2017). For example, the aquatic plants in Poyang Lake, Hongze Lake, and Honghu Lake have decreased by 46%, 72% and 84%, respectively since 1983 (Zhang et al., 2017). In Taihu Lake, the total area of aquatic plants decreased from 297.68 km^2 (2004) to 224.55 km^2 (2013) (Luo et al., 2016). Although there has been considerable progress made to understand the macrophyte changes in this region, many of the studies focus only on the recent ecological problems rather than their deep historical causes (Tao et al., 2010; Zhang et al., 2010; Luo et al., 2016). The temporal variability of aquatic plants at multi-decadal time scales is still poorly understood.

In this paper, we use palynological records to provide a detailed history of aquatic plants in Changdang Lake in the Middle and Lower Yangtze River Basin. Changdang Lake has experienced serious degradation during the past several decades (Wang et al., 2012; Cai et al., 2014). Zhang et al. (2018) used lipid biomarkers and other geochemical proxies to investigate Changdang Lake and found two eutrophication phases since the 1950s. However, how the aquatic plants changed through time is not clear from the Zhang et al. (2018) record, such as the composition and structural changes of different aquatic plant communities (emergent/floating/submerged types), which is crucial for sustainable lake ecosystem restoration and management. Here, we focus on three key questions: (1) what are the long-term trajectories of aquatic plants changes? (2) when did the key transitions between different aquatic plant communities occur? and (3) what are the potential driving factors that influence the succession of aquatic plants? Moreover, this study aims to determine the current state of the aquatic ecosystem in Changdang Lake and provide potential management strategies for future ecological restoration.

2. Study area

2.1. Environmental and climatic conditions

Changdang Lake (31° 33′-31° 40′ N, 119° 30′-119° 37′ E) is located in the east of the Middle and Lower Yangtze River Basin, between Jintan District and Liyang City, and lying to the west of Gehu Lake and Taihu Lake (Fig. 1). The lake is 16 km long and 9 km wide with an area of about 90 km^2, a mean depth of 0.8–1.2 m and a water retention time of approximately 55 days (Cai et al., 2014). Changdang Lake is hydrologically connected with 12 rivers and tributaries. The terrain in the lake area is high in the west and low in the east due to Maoshan Mountain (Fig. 1), thus most inflowing rivers are from the west and the outflows generally flow into Gehu Lake and from there to Taihu Lake (Wang et al., 2012). During the 1970s–1980s, a series of new dams and watercourses were built and intensive lake reclamation for farming occurred around Changdang Lake, significantly altering the local landscape (Compiling Team for Annals of Jintan County, 1993). Changdang Lake is mainly affected by a warm-humid subtropical monsoon climate, belonging to the Cfa class in the Köppen−Geiger Climate Classification (Kottek et al., 2006). The rainfall (mean annual precipitation 1151.1 mm; China Meteorological Data Service Center, CMDC) from April to September is the main factor influencing the water level of Changdang Lake. The region's prevailing wind direction is southeast and east (Peng et al., 2016).

2.2. Aquatic plants

There are abundant aquatic plant resources in Changdang Lake due to the favorable climatic and hydrological condition. Dominant aquatic plants are classified by different growth forms and listed in Table 1. All aquatic plants can be divided into three vegetation zones. Zone 1 is 5–10 m wide and located near the lake shoreline, with the aquatic vegetation mainly composed of marsh and emergent plants including Cyperaceae, *Polygonum*, *Phragmites*, and *Zizania* (Fig. S1a and b). Zone 2 consists of floating-leaved and free-floating plants, such as *Nymphoides*, *Trapa*, and *Azolla*, distributed sporadically within a limited area in river channels or intermediate zones between the lakeshore and open water (Fig. S1a, c, and d). Zone 3 is dominated by various submerged plants, especially *Potamogeton* types, occupying most areas of the lake (Zhu, 1989). However, zone 3's area has declined significantly in recent years according to our 2017 survey (Fig. S1a and e; Table S1).